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NORTH AMERICAN COTTONWOODS (POPULUS, SALICACEAE) OF SECTIONS ABASO AND AIGEIROS

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AS A RESULT of research on *Populus* L. in southwestern North America (including Mexico), I have made taxonomic decisions that require changes of name for several cottonwoods. The following review, while not monographic in scope, provides sufficient evidence to justify the new status accorded to several well-known taxa, as well as to warrant the description of a new section and a new subspecies in this rather crowded small genus. The morphological, distributional, ecological, and paleobotanical information used here to substantiate these innovations may contribute to further discussion of the systematics of these conspicuous but poorly understood trees.

In addition to major synonyms, I have included major misapplied names. These *sensu* names, which have no direct nomenclatural status, are too often intermingled with the true nomenclatural synonyms. Nonetheless, these misapplications may be of considerable interest for taxonomy, and I have followed Recommendation 50D of the International Code of Botanical Nomenclature for their presentation. I have also included a key to all sections of the genus. This should help to clarify the mutual relations of these taxa and to place the newly described sect. ABASO. The key to cottonwoods of sect. AIGEIROS is the first to include all extant North American taxa.

WORLD KEY TO SECTIONS OF POPULUS

A. Anthers elongate, apiculate at apex; disc of female flower deeply lobed or laciniate.
  B. Plants with markedly heteroblastic leaf development: leaves of juvenile plants linear, those of adults broader; disc of female flower caducous.
    C. Leaves entire or with few large, coarse teeth; carpels (2–)3; ovules >30 per placenta. ..... sect. TURANGA Bunge.
    C. Leaves minutely serrate for most of their length; carpels 2(–3); ovules <15 per placenta. ..... sect. ABASO Eckenwalder.
  B. Plants without markedly heteroblastic leaf development: leaves of both juvenile and adult plants broadly ovate; disc of female flower persistent

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or only tardily deciduous. ..... sect. LEUCOIDES Spach.

A. Anthers short and broad, truncate or emarginate at apex; disc of female flower with entire margin, or slightly sinuately lobed, or minutely dentate.
D. Winter buds only slightly resinous or densely tomentose; floral bracts ciliate; stamens 5–12(–20); disc of female flower narrowly cup-shaped, usually markedly oblique; stigmas 2- or 3-lobed, segments linear; carpels 2. .... sect. POPULUS (= sect. LEUCE Duby) (aspens, white poplars).
D. Winter buds very resinous, if pubescent then not tomentose; floral bracts not ciliate; stamens (8–)20–80; disc of female flower broadly cup-shaped or reduced, only slightly oblique; stigmas 2-lobed, segments broadly expanded, sometimes convoluted; carpels 2–4.
E. Leaves generally not deltoid, markedly heterolateral: upper surface dark bright green, lacking a narrow translucent margin; lower surface white, glaucous, often somewhat discolored by streaks of orange resin; petioles terete, often channeled above. ..... sect. TACAMAHACA Spach (balsam poplars).
E. Leaves ± deltoid, not heterolateral: both upper and lower surfaces light green, with a narrow translucent margin, not markedly glaucous beneath, sometimes marked by streaks of milky resin; petioles laterally compressed near junction with leaf blade (or, if resembling sect. TACAMAHACA in some of these characteristics, the leaves markedly deltoid to trullate). ..... sect. AIGEIROS Duby (cottonwoods, black poplars).

Populus sect. Abaso Eckenwalder, sect. nov.

Gemmae hyemales leviter viscosae, crassae, stramineae; bracteolae lineares, laciniatae ad apices; perigonia florum marum vadose cyathiformia, obliqua, lobata; stamina apiculata; perigonia florum femineorum praealte cyathiformia caduca e zona abscissionali bene evoluta, tenuissima, e base ad latum divisa, laciniata; capsulae bivalvae (raro trivalvae); stylum unicus; stigmata aliquantum tumida, cucullata, convoluta.

SPECIES TYPICA: *Populus mexicana* Wesmael.

Abaso is the Cáhita folk name for *P. mexicana*. This species is most abundant in the Cáhita territory of Sonora and Sinaloa. No other extant species of the section is known at present.

All authors from Wesmael (1868) to Wiggins (1964) who have treated *Populus mexicana* have evidently considered it a member of sect. AIGEIROS. Most of these authors had only sterile material or mature capsules available. Leaves of adult trees of *P. mexicana* are broadly deltoid and long-acuminate. They somewhat resemble those of sect. AIGEIROS, cottonwoods, especially those of *P. nigra* L. of Eurasia and North Africa. The capsules are also superficially reminiscent of those of members of sect. AIGEIROS, so assignment to this section was quite reasonable. However, examination of flowering material from my own and other collections shows that the floral and vegetative characteristics of *P. mexicana* contrast strongly with those of sect. AIGEIROS. The apiculate anthers and laciniate, caducous disc of the female flowers in *P. mexicana* contrast with the

emarginate anthers and entire, sometimes reduced, persistent disc usual in sect. AIGEIROS. The juvenile leaves, which are linear in *P. mexicana* and rhomboid in members of sect. AIGEIROS, can also be used to distinguish the two taxa. Furthermore, winter buds of *P. mexicana* are stout, blunt, dry, and bright yellow and differ from the elongated, sharp-pointed, resinous, tan to red buds of the AIGEIROS cottonwoods. Lastly, *P. mexicana* has more numerous catkins per shoot (often 10–15) than do the AIGEIROS cottonwoods (usually 2–5), and it sometimes has a leaf on the proximal portion of the catkin, a primitive condition never found in representatives of sect. AIGEIROS.

These characteristics of *Populus mexicana* resemble those of species of sect. TURANGA (including sect. TSAVO (Jarmolenko) Browicz) of the old-world tethyan arid zone from Spain and Morocco to Mongolia. The new-world plants, however, differ from those of the Old World in their different leaves as well as in their much lower seed number and fewer carpels. Furthermore, the old-world *P. euphratica* Oliver and its allies invariably display sympodial growth with abortion of the shoot apex (Kimura, 1938; Browicz, 1966), while this habit is only incompletely established in sect. ABASO. Sections ABASO and TURANGA are more strongly separated than the universally accepted sects. AIGEIROS and TACAMAHACA, which differ only in vegetative characters. Differences between sects. ABASO and LEUCOIDES are even greater, and there is little beyond generic resemblance between sect. ABASO and sects. POPULUS and TACAMAHACA.

Poplars resembling sect. ABASO are first known from the Eocene Green River Formation of Colorado, Utah, and Wyoming. *Populus cinnamomoides* (Lesquereux) MacGinitie (= *P. wilmattae* Cockerell), known only from leaf remains, has the narrow juvenile leaves and broad, long-acuminate adult leaves of sect. ABASO, as well as similar details of venation (MacGinitie, 1969; Eckenwalder, unpubl.). Similar leaves have been found in nearly contemporaneous deposits of the Puget Group in Washington (J. A. Wolfe, pers. comm.) and in the Claiborne Flora of Texas and Tennessee (Berry, 1916, 1930; as *Banara eocenica* Berry (Flacourtiaceae) and *Grewiopsis tennesseensis* Berry (Tiliaceae)). Beyond continued presence in Oligocene deposits of the Ruby Basin of Montana (Becker, 1972; Eckenwalder, unpubl.), this section has no further known fossil record, leaving a gap of more than 25 million years between the last known fossil occurrence and the present.

Populus mexicana Wesmael in DeCandolle, Prodromus **16**(2): 328. 1868. TYPE: Mexico, entre Tampico [Tamaulipas] et Real del Monte [Hidalgo], May 1827, *Berlandier 274* (holotype, G–DC (IDC B-800. 2766: I. 1.!); isotypes, G, MO!).

This species, with its strongly heteroblastic leaf development marked by distinctive willow-like leaves of the juvenile phase, consists of two subspecies, one from each coast of Mexico. I include an illustration of this species (FIGURE 1), which has not heretofore been figured.

FIGURE 1. *P. mexicana* subsp. *dimorpha*: A, flowering shoot; B, ♂ catkin; C, ♂ flower with bract; D, stamen; E, ♀ catkin; F, ♀ flower with bract; G, fruiting catkin; H, inside of capsule valve showing seed attachments; I, shoot of juvenile plant; J, mature adult leaf. *P. mexicana* subsp. *mexicana*: K, mature adult leaf. (A–D from *J. E. Eckenwalder 17*; E, F from *J. E. Eckenwalder 22*; G, H, J from *J. E. Eckenwalder 397*; I from *J. E. Eckenwalder 20*; K from *J. E. Eckenwalder 448*. All specimens at UC.)

Populus mexicana subsp. **mexicana.**

Populus arizonica auct. non Sargent; Miranda, La vegetación de Chiapas **1:** 143, 145, 146, 184, 185. 1952.

This cottonwood has been poorly understood ever since its description in 1868. Wesmael (1869) himself expressed doubts as to its distinctness from *P. nigra* of Europe and subsequently (1887) placed it in the synonymy of the later described *P. fremontii* S. Watson. The name *P. mexicana* was often misapplied to *P. fremontii* subsp. *mesetae* Eckenwalder, the AIGEIROS cottonwood of the central plateau of Mexico, in herbarium identifications (Sargent, 1902 and 1919a). The type material (*Berlandier 274*), although sterile, clearly belongs to the uncommon but widespread ABASO cottonwoods of rivers of the Gulf of Mexico Coastal Plain from near Monterrey to the state of Veracruz. *Populus mexicana* subsp. *mexicana* also occurs in mountains of Oaxaca and Chiapas (the southernmost station for *Populus* in the New World). This cottonwood has often been misidentified in herbaria as *P. arizonica* Sargent (= *P. fremontii* subsp. *fremontii*) of sect. AIGEIROS, from which it differs in the lack of pubescence on shoots, buds, and leaves, in addition to characteristics given in the sectional key.

Populus mexicana subsp. **dimorpha** (T. S. Brandegee) Eckenwalder, comb. et stat. nov.

Populus dimorpha T. S. Brandegee, Zoë **5:** 197, 198. 1905. TYPE: Mexico, Sinaloa: Culiacán, 20 Aug. 1905, *T. S. Brandegee s.n.* (holotype, UC!; isotypes (dated *22* Aug.), F!, GH!, NY!, POM!).

Because of the obscurity surrounding the identity of *Populus mexicana* subsp. *mexicana* (Standley, 1920), and also because the willow-like juvenile leaf phase which Brandegee noted for his plants (and used as the basis for his epithet) has hitherto been unknown in the typical subspecies, no previous author has admitted a relationship between the uncommon trees of eastern Mexico and the abundant cottonwood of Coastal Plain rivers of the west. One Veracruz specimen, however, was identified as *P. dimorpha* by the Flora of Veracruz project. Nonetheless, the two populations agree in most features of floral structure, as well as in shoot and bud characters and in their pattern of heteroblastic leaf development. They differ in the predominant leaf shape of adult trees, with leaves of subsp. *dimorpha* longer acuminate than those of subsp. *mexicana* (FIGURE 1J, K). They also differ in number of ovules per placenta of otherwise similar capsules (6–9 in subsp. *mexicana*, (8–)11–15 in subsp. *dimorpha*). The southern inland populations of Oaxaca and Chiapas are somewhat intermediate in these characteristics, further strengthening the link between the two taxa. *Populus mexicana* subsp. *dimorpha* occurs on floodplains of all major perennial rivers of the western Coastal Plain from the Rio Yaqui (Edo. Sonora) to the Rio Piaxtla (Edo. Sinaloa). It is abundant in the northern valleys, although quite rare from the Rio San Lorenzo (Edo. Sinaloa) southward.

Populus sect. **Aigeiros** Duby, Botanicon Gallicum 1: 428. 1828. TYPE: *Populus nigra* Linnaeus, Sp. Pl. 2: 1034. 1753.

These are the lowland riparian cottonwoods of the great rivers from coast to coast across the central portion of North America. Different authors have recognized from one to ten species of this section in southwestern North America (Sargent, 1922). With removal of *P. mexicana* into sect. ABASO, the remaining taxa form a rather homogeneous group, which has been designated subsect. AMERICANAE Bugała (1967) in contradistinction to the old-world subsect. EUROASIATACAE Bugała. These cottonwoods are characterized by large, tan, setose, resinous winter buds, many stamens, 3–4-carpellate, glabrous ovaries, and large, platelike stigmas. The distinctive early leaves (those of the spring flush) of all are broadly deltoid-ovate, coarsely crenate-dentate in the middle portion, and with an abrupt, long, toothless, acuminate apex. Within this framework of similarity, however, there are substantial differences between local populations (Marcet, 1962). Among characters that show considerable variation are various aspects of leaf shape (FIGURE 2), basilaminar glands, pubescence, pedicel length, stamen number, disc shape and width, capsule shape, and ovule number. The distribution of variation can be divided geographically in many ways, which accounts in part for the diversity of species treatments in this group. Geographic variation patterns of several characters are only partially correlated, but disc width and some other floral characteristics seem to follow broad geographic outlines. Each population occupying a distinct drainage system has a distinctive facies, although, insofar as is known, all populations are fully interfertile (Stout & Schreiner, 1933; Zsuffa, 1975; Eckenwalder, unpubl.). These populations cohere into five major geographic races worthy of formal taxonomic recognition, and the races can be further grouped into eastern and western taxa. On this basis, I recognize only two extant species of North American AIGEIROS cottonwoods, each with subspecies. The geographic boundaries between these species and subspecies are zones of character state shift for the greatest number of characters.

Fossilized leaves from western North America attributable to sect. AIGEIROS are widespread in Pliocene deposits where they have been assigned names such as *Populus prefremontii* Dorf and *P. lamottei* Chaney & Elias (LaMotte, 1952). The only earlier remains known are specimens of *P. russellii* Knowlton from late Miocene horizons of the Ellensburg Flora of central Washington (Smiley, 1963). None of these forms, in the absence of reproductive material, shows particularly close relationships to either of the extant species, although they are quite similar to both. Pleistocene remains, equally undiagnostic, have been assigned to extant taxa (LaMotte, 1952; Axelrod, 1966).

KEY TO NATIVE NORTH AMERICAN TAXA OF SECT. AIGEIROS

A. Floral disc broad in fruit, 5–9 mm. wide, deeply cup-shaped; pedicels short, 4 mm. long; young shoots and petioles often pubescent. . . *Populus fremontii.*

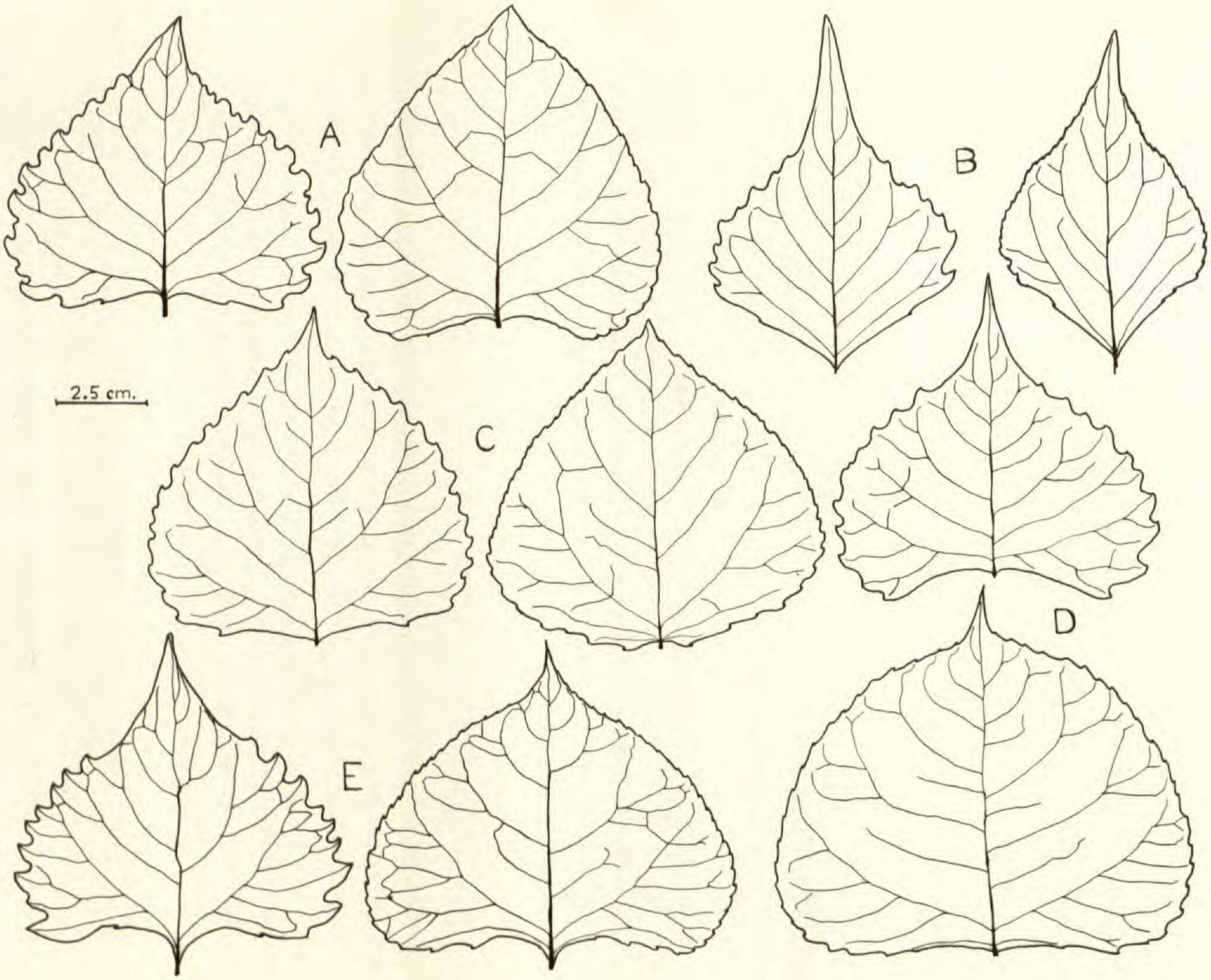

FIGURE 2. Representative early leaves (left or above) and late leaves (right or below) of native North American sect. AIGEIROS cottonwoods: A, *P. fremontii* subsp. *fremontii*, *J. E. Eckenwalder 904* (UC); B, *P. fremontii* subsp. *mesetae*, *J. E. Eckenwalder 408* (UC); C, *P. deltoides* subsp. *deltoides*, *J. L. Strother 1226* (UC); D, *P. deltoides* subsp. *monilifera*, *D. S. Correll & I. M. Johnston 17103* (TEX); E, *P. deltoides* subsp. *wislizenii*, *J. E. Eckenwalder 237* (UC).

B. Shoots with orange cast, usually densely pubescent; late leaves (those initiated and expanding during current growing season) and early leaves of slender and lateral shoots often trullate, cuneate at base, longer than wide, long-acuminate. ..... *P. fremontii* subsp. *mesetae*.

B. Shoots with yellow or gray cast, glabrous to densely pubescent; late leaves broadly deltoid, usually truncate or cordate at base, occasionally broadly cuneate, often as wide as or wider than long, short-acuminate or acute. ..... *P. fremontii* subsp. *fremontii*.

A. Floral disc reduced in fruit, 1–4 mm. wide, flat to shallowly cup-shaped; pedicels short to long, ⩽15 mm. long; shoots and petioles glabrous. ..... *Populus deltoides*.

C. Pedicels uniformly short, <6 mm. long; leaves often long-acuminate, usually with 2 basilaminar glands (or none). ..... *P. deltoides* subsp. *monilifera*.

C. Pedicels longer, up to 15 mm. long; leaves usually short-acuminate, with 0–5 basilaminar glands.

D. Pedicels nearly uniformly long along the catkin; leaves without basilaminar glands; late leaves broadly deltoid, usually as wide as or wider than long; winter buds pubescent; emergent leaves glabrous. ..... *P. deltoides* subsp. *wislizenii*.

D. Pedicels long proximally, much shorter distally along the catkin; leaves usually with 3–5 basilaminar glands; late leaves broadly ovate, usually distinctly longer than wide; winter buds glabrous; emergent leaves pilose. ..... *P. deltoides* subsp. *deltoides*.

Populus fremontii S. Watson, Proc. Am. Acad. Arts **10**: 350. 1875. SYNTYPES: California, Tehama Co., Deer Creek at Lassen's, 1846, *Fremont 243* (♀) and *244* (♂) (lectotype (here designated), *243* (♀) at GH; isolectotype, NY!).

This species is treated by various authors either as the sole southwestern AIGEIROS cottonwood (Little, 1953) or as a Californian representative of a series of local species (Sudworth, 1934). The broader view adopted here emphasizes the similarities of diverse populations of this species in possessing short pedicels and in the broad, cup-shaped floral disc enclosing the lower portion of the fruit. In addition, most individuals have globose capsules and more or less yellowish-green leaves that are tomentose with short, yellow-tinged hairs, as are the first-year shoots, although glabrous individuals are fairly common, especially in northern California. Furthermore, there is a tendency for leaves of *Populus fremontii* to be smaller and thicker than those of *P. deltoides*, as well as to have fewer teeth and a shorter apex (FIGURE 2), but there is much overlap in these characteristics. Variation within *P. fremontii* seems best treated by segregating populations from east and west of the continental divide as two subspecies, a disposition which has in essence been followed by authors who have treated these population systems as two species, *P. fremontii* and *P. arizonica* Sargent (Johnston, 1944).

Populus fremontii subsp. **fremontii**

Populus macdougalii Rose, Smithson. Misc. Collect. **61**(12): 1, 2. 1913.
Populus arizonica Sargent, Bot. Gaz. (Crawfordsville) **67**: 210. 1919.
Populus arizonica var. *jonesii* Sargent, *op. cit.* 211.
Populus fremontii var. *pubescens* Sargent, *op. cit.* 213.

These plants vary from quite glabrous for many trees of northern cismontane California, to densely pubescent in the Mojave Desert and other regions. In general, this subspecies is much more variable than is the following, with several distinctive local variants. For instance, many trees of the lower Colorado River and the Salton Basin have the floral disc of the fruit much reduced, and in this respect resemble *Populus deltoides*. These trees have been segregated as *P. macdougalii*, but a broad spectrum of intermediates between them and "typical" *P. fremontii* occurs in this same region. Similarly, juvenile individuals with rhomboid rather than deltoid leaves occur scattered throughout the range, and are referred to *P. arizonica* in California (Munz, 1959). Much of this and other variation in leaf form can be attributed to the diameter of the shoot (and ultimately of the shoot apex) that bore them, as pointed out by Dode (1905). In general, trees of subsp. *fremontii* have larger, very broad, deltoid early and late leaves with truncate or cordate bases, and may thus be distinguished from subsp. *mesetae* (FIGURE 2A, B). In this broad view, *P. fremontii* subsp. *fremontii* occurs west of the continental divide from the rim of the Sacramento Valley (California) and the western flanks of the Wasatch Range (Utah), south through Arizona to northern Baja California and Sonora, with outliers in Nevada and southwestern New Mexico.

Populus fremontii subsp. **mesetae** Eckenwalder, subsp. nov.

Populus mexicana auct. non Wesmael; Sargent, Silva of North America **14**: 73, 74. *pl. 733*. 1902.
Populus arizonica auct. non Sargent; Johnston, Jour. Arnold Arb. **25**: 434, 435. 1944. Correll, Flora of Texas **3**: 397–399. *pl. 58*. 1961.

A *P. fremontii* typica differt statura aliquantum inferiore; pubescentia ramuli novelli ochracea, confertiore; foliis aestivalibus trullatis non deltoideo-ovatis, base cuneatis vel rotundatis, rariore truncatis, non subcordatis; bracteolis angustioribus.

TYPUS: Mexico. Chihuahua: Valley near Chihuahua, 31 Mar. 1886, *Pringle 885* (holotype, UC!; isotypes, F!, GH!, MO!).

Populus fremontii subsp. *mesetae* derives its name from the Meseta Central of Mexico where it is primarily distributed.

Tree 6–20 m. tall, 2–12 dm. d.b.h.; trunk dividing near base into 2 or 3 major branches, ascending at a low angle and spreading to form a broad oval crown; bark tan and deeply furrowed at base, bone white to light tan and smooth on branches. First year twigs tan, usually densely pubescent with short, soft, ochraceous hairs. Winter buds ovate, yellow-brown,

resinous, sparsely to densely pubescent with short, stiff hairs; terminal vegetative buds and female flowering buds 7–12 mm. long; male flowering buds 11–20 mm. long. Leaf blade yellow green, (2–)4–14 cm. long; early leaves of main shoots broadly deltoid-ovate, about as wide as long, with truncate or subcordate base and short-acuminate, entire apex; late and early leaves of weak shoots trullate, about ¾ as wide as long, with cuneate (rarely truncate) base and long-acuminate, entire apex (FIGURE 2B). Early leaves coarsely serrate with 3–15 crenate teeth on each side of blade; late leaves finely serrate with 10–25 small teeth on each side; petiole 1–9 cm. long, transversely flattened at junction with leaf blade, pubescent. Aments 4–13 cm. long, lax, with 10–30 flowers. Stamens 30–70. Capsule 6–10 mm. long, broadly ovoid to globular, obtuse, 3–4-valved, with 11–18 ovules per placenta; disc 5–8 mm. broad, cup-shaped, enclosing lower portion of fruit; fruiting pedicel 1–3 mm. long. Flowering February to April, fruit maturing April to July.

This cottonwood is common along major rivers of the basins and in canyons of the foothills throughout much of the Chihuahuan Desert region. It extends, mostly east of the continental divide, from southern New Mexico and trans-Pecos Texas south on the Central Plateau to the Valley of Mexico, with a possible outlier in the Chiricahua Mountains, Arizona. Much of its southern distribution appears to be anthropogenic, and it is widely planted about ranches and in towns throughout the region. Isolated individuals are commonly found near springs and other small, perennial sources of water.

Unfortunately, none of the five epithets applied to this well-known tree in the literature and in herbaria can be used under the taxonomic concepts accepted here. Most herbarium specimens are identified as *Populus mexicana* or *P. arizonica*; others as *P. fremontii*, *P. wislizenii* (S. Watson) Sargent, or *P. arizonica* var. *jonesii* Sargent. Johnston (1944) discussed the nomenclature of this cottonwood, which he considered a species distinct from *P. fremontii*. He decided in favor of the name *P. arizonica* Sargent, which he lectotypified by *Pringle 885*, a Chihuahuan specimen. This specimen probably served as the basis for part of *plate 773* of "P. mexicana" in Sargent (1902). Sargent (1919a), after examining a photograph of the type of *P. mexicana* Wesmael, had proposed the name of *P. arizonica* for the cottonwood described as "P. mexicana" in 1902. Thus Johnston argued that *P. arizonica* should be typified by the "major element" in the plate of "P. mexicana" in Sargent (1902). This lectotypification is untenable, however, because Sargent (1919a) specifically excluded *Pringle 885* from *P. arizonica* var. *arizonica*, and assigned it instead to *P. arizonica* var. *jonesii*, described concurrently. The Arizona syntypes of *P. arizonica* are all referable to typical *P. fremontii*. While Sargent assigned all specimens of *P. fremontii* subsp. *mesetae* to *P. arizonica* var. *jonesii*, the type of this variety, *M. E. Jones 3731*, from Baja California, is another specimen of typical *P. fremontii*. Other epithets in the complex are based on specimens from California, Arizona, or New Mexico and

are all referable to *P. fremontii* subsp. *fremontii* as circumscribed here. Thus it is necessary to name here the prominent cottonwood of the arid Mexican plateau, a tree which is one of the largest in the region, is widely planted in the alamedas of Mexican towns, and has been well known to plant explorers for at least a century.

Populus deltoides Bartram ex Marshall, Arbustrum Americanum 103. 1785. TYPE: Carolina and Florida, *W. Bartram* (holotype, BM? (not located)).

Populus canadensis auct. non Moench; Kuntze, Rev. Gen. Pl. 643. 1891.
Populus balsamifera auct. non Linnaeus; Farwell, Rhodora **21:** 101. 1919. Sargent, Jour. Arnold Arb. **1:** 62, 63. 1919.

The taxonomy and nomenclature of this species are rather confused as a result of its early introduction into Europe and of its spontaneous and artificial hybridization there with *Populus nigra* L. Different introductions and hybrids of various provenances each received separate names in the late eighteenth and early nineteenth centuries. In general, however, most European and many American authors have recognized a southern and a northern cottonwood in the eastern United States (Schneider, 1906; Sargent, 1922), although they have not all agreed on the proper names for the two taxa. *Populus canadensis* Moench has occasionally been used for the eastern cottonwood when *P. deltoides* was considered an ambiguous name, but it seems more properly referable to the Euro-American hybrids between *P. deltoides* and *P. nigra* (Boom, 1957). The most awkward nomenclatural upset arose when Sargent (1919b) and Rehder (1927, 1929) adopted Farwell's (1919) suggestion that *P. balsamifera* applied to the eastern AIGEIROS cottonwood, rather than to the eastern TACAMAHACA balsam poplar. This assertion was finally laid to rest by Rouleau (1946), and *P. deltoides* has since remained unchallenged as the name of the eastern cottonwood (Little, 1953).

As defined here, *Populus deltoides* consists of three intergrading subspecies that are distinguished by pedicel, pubescence, and leaf characters outlined in the key. As with *P. fremontii*, each subspecies is quite variable, although the subspecies resemble each other in the long-ovate to elliptic capsules that are subtended by very reduced floral discs and are often borne on highly elongated pedicels, in the darker green leaves that are often larger than those of *P. fremontii*, and in the glabrous shoots. Some aspects of leaf morphology, such as shape, number of teeth, and number of basilaminar glands, show clinal, or even seemingly random, variation (Marcet, 1962; Eckenwalder, unpubl.). Within this context, boundaries of the subspecies enclose the most homogeneous populations with the greatest association of characters.

Populus deltoides subsp. **deltoides**

Populus virginiana Fougeroux, Mém. Agric. Soc. Roy. Agric. Paris 1786. 87–90. 1787.

Populus angulata W. Aiton, Hortus Kewensis **3:** 407. 1789.
Populus angulata var. *missouriensis* A. Henry in Elwes & Henry, Trees of Great Britain and Ireland **7:** 1811. 1908.

This is the "southern" cottonwood, which extends from the Gulf Coast states northward along the Atlantic seaboard to Massachusetts and northward in the Mississippi embayment region to central Illinois and Ohio. It occurs westward as far as eastern Texas and Oklahoma. Marcet (1962) postulated relatively recent occupation of the northern portion of this range at the expense of the more northerly subsp. *monilifera*, but this, while possible, is not clear from the evidence. *Populus deltoides* subsp. *deltoides* is characterized by its glabrous winter buds and densely pilose emerging leaves and differs from the other two subspecies in its relatively long, broadly ovate, late leaves (FIGURE 2C) with 3–5 tubular basilaminar glands. Early leaves are often quite similar in shape and marginal teeth to those of subsp. *wislizenii*, and the pedicels reach the length of those of subsp. *wislizenii*, but they are more variable in length on the same catkin. Apical pedicels are as short as those of subsp. *monilifera*, but they become longer basipetally (subsp. *monilifera* has uniformly short pedicels within a catkin). The early leaves tend to have shorter points and may have fewer teeth than those of subsp. *monilifera*.

Populus deltoides subsp. **monilifera** (W. Aiton) Eckenwalder, stat. nov.

Populus monilifera W. Aiton, Hortus Kewensis **3:** 406. 1789. TYPE: (Canada) cult. Kew Gardens, *W. Aiton* (holotype, BM!).
Populus deltoides var. *occidentalis* Rydberg, Mem. New York Bot. Gard. **1:** 115. 1900.
Populus sargentii Dode, Bull. Soc. Hist. Nat. Autun **18:** 198. 1905.
Populus deltoides var. *monilifera* (W. Aiton) A. Henry, Gard. Chron. Ser. 3. **56:** 2. *fig. 4.* 1914.
Populus texana Sargent, Bot. Gaz. (Crawfordsville) **67:** 211, 212. 1919.

Most modern discussion of *P. deltoides* has revolved around the distinctness of the cottonwoods of the Great Plains region from their eastern counterparts (Fowells, 1965). The contrasts of foliar and bud characteristics usually advanced to distinguish a western species (*P. sargentii*) or variety (*Populus deltoides* var. *occidentalis*) from the eastern cottonwood (Sargent, 1913) really apply solely to the southern cottonwood, *P. deltoides* subsp. *deltoides*. The cottonwoods of the Great Lakes and other representatives of the northern cottonwood are, in fact, quite similar to the trees of the plains, and I treat them all as members of a single subspecies. They are similar in their short pedicels, pubescent winter buds. and long-acuminate, deltoid-ovate leaves (FIGURE 2D), generally with a single pair of basilaminar glands (although these are absent in a few Texas plants). There is a general decline in tooth number southwestward from the northeastern part of its range. This subspecies occurs from the

Great Lakes region westward to the Prairie Provinces and south to the Texas panhandle.

Populus deltoides subsp. **wislizenii** (S. Watson) Eckenwalder, comb. et stat. nov.

Populus fremontii var. *wislizenii* S. Watson, Am. Jour. Sci. **15:** 137. 1878. TYPE: New Mexico, on the Rio Grande near Charvis and lower down, below Santa Fe, 20 July 1846, *A. Wislizenus s.n.* (holotype, GH; isotype, MO!).

Populus wislizenii (S. Watson) Sargent, Silva of North America **14:** 71, 72. *pl. 732.* 1902.

Whether they treat the cottonwoods of the upper Rio Grande valley as a separate species (Standley, 1920) or as a variety of *P. fremontii* (Little, 1953), most authors have indicated that these trees have their greatest affinity with the western *P. fremontii.* Little (1971) went so far as to include the distribution of this subspecies as part of that of *P. fremontii* without differentiation in his distribution maps. Only Correll (1961) has pointed out the similarities of these trees to the cottonwoods of the Great Plains, which he treated as the segregate *P. sargentii.* Shoot, bud, and capsule characters all align this subspecies with the eastern *P. deltoides* rather than with *P. fremontii.* Like those of *P. fremontii*, leaves of *P. deltoides* subsp. *wislizenii* lack basilaminar glands but are generally broader (especially the juvenile leaves) with fewer, coarser teeth (FIGURE 2E), features that also distinguish them from leaves of other subspecies of *P. deltoides*. These trees are further distinguished by the uniformly elongated fruiting pedicels.

Populus deltoides subsp. *wislizenii* occupies the upper Rio Grande drainage from near El Paso northward and extends to the Colorado River drainage in northeastern Arizona, eastern Utah, and western Colorado. While the southwestern boundary between this subspecies and *P. fremontii* is quite sharp, there is a narrow zone of intergradation between these taxa in eastern Utah, and there is a broader zone of intergradation of subsp. *wislizenii* and subsp. *monilifera* in southeastern Colorado and adjacent New Mexico and Oklahoma. These zones presumably represent areas of hybridization between mutually fully compatible taxa (Zsuffa, 1975; Eckenwalder, unpubl.), and I postulate further local hybridization between *P. deltoides* subsp. *wislizenii* and *P. fremontii* subsp. *mesetae* in the vicinity of the Davis Mountains in trans-Pecos Texas to account for variation patterns in this area.

The generalized distributions of these species and subspecies outlined above are far from definitive. The distributions (partly derived from those of Sudworth, 1934, and Little, 1972) and the original taxonomic framework presented here are largely based on the abundant, but too often poor, material available in herbaria. Characteristics of few populations are well documented in the collections of any herbarium, and I urge anyone wishing to contribute specimens of this group (and of *Populus*

generally) to gather as full material as possible, ideal documentation requiring three separate collection times. Male and female flowering material appears in early spring (February–April), fruiting material in late spring (May–June). Winter buds mature in late summer (August–October) before the fully mature leaves drop in autumn. Characters useful in the taxonomy of cottonwoods are drawn from this complete phenological cycle. It is important in gathering leaf material to gather whole long shoots (from last year's bud scale scars to the shoot apex), since early leaves (those of the spring flush) often differ in form from late leaves (those produced during the current growing season; Critchfield, 1960), and both types show useful taxonomic characters. Midsummer collections with neither fruits nor winter buds and winter collections showing only shoot characteristics are, unfortunately, rather more common in herbaria than the more useful kinds of specimens described above. Further progress in cottonwood systematics will depend, in large part, on better documentation of many populations along the lines suggested here.

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